

SEED-SIZE SELECTION IN MOURNING DOVES AND EURASIAN COLLARED-DOVES

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ABSTRACT.—I studied seed-size selection among Mourning Doves (*Zenaida macroura*) and Eurasian Collared-Doves (*Streptopelia decaocto*), two newly sympatric species for which mechanisms of seed selection are not well understood. I measured and compared mean length, breadth, and thickness of seeds available to, and consumed by, these species in feeding trials of penned birds. Both species selected corn (*Zea mays*) seeds that were shorter and narrower than average, but Eurasian Collared-Doves selected corn that was thicker than average and sunflower (*Helianthus annuus*) seeds that were broader and thicker than average. Mourning Doves consumed corn of average thickness, and wheat (*Triticum aestivum*) and sunflower seeds of average size with respect to all dimensions. Corn consumption by both species seems limited by seed length and breadth, but Mourning Dove consumption of smaller seed types (wheat and milo [*Sorghum vulgare*]) appears largely unaffected by seed size. Among larger seed types (corn and sunflower), Eurasian Collared-Doves may select thicker- and/or broader-than-average seeds to maximize foraging efficiency. Sunflower and corn seeds consumed did not vary between species with respect to any dimension, but Eurasian Collared-Doves seemed willing to select, and able to eat, broader and thicker seeds than Mourning Doves, which may limit foraging competition between these species. Received 7 February 2005, accepted 23 November 2005.

Seed selection by granivorous birds is a complex phenomenon potentially affected by a number of factors (Ramos 1996), the relative contributions of which remain poorly understood in many avian granivores. In particular, seed selection by doves and other species that do not husk seeds before swallowing is not well understood; most studies of seed selection in birds have focused on finches and other species that husk seeds during the course of foraging. Generally, these studies have revealed that the physical characteristics of seeds affecting handling time, such as size, shape, and hardness, are important determinants of preference, and that nutritional composition of foods appears relatively unimportant (Willson 1971, Willson and Harneson 1973, Goldstein and Baker 1984, De Nagy Koves Hrabar and Perrin 2002), especially without consideration of the overall economics of nutrient intake and the factors affecting it (Greig-Smith and Wilson 1985).

One approach to understanding the effect of seed size on selection has been to examine size selection by one or more species for a single seed type (Hespenheide 1966, Myton and Ficken 1967, Willson 1972, Abbott et al. 1975, Greig-Smith and Crocker 1986, van der Meij and Bout 2000). A number of these studies have indicated seed-size preference within

a species (Greig-Smith and Crocker 1986, van der Meij and Bout 2000), and/or correspondence between size selection and bill size among multiple species (Hespenheide 1966, Myton and Ficken 1967, Willson 1972). One study indicated no size preferences and/or no seed size/bill size correspondence (Abbott et al. 1975), but this study focused on a seed-husking species. Because doves and pigeons have relatively long slender bills and pecking behaviors that maximize speed of seed intake without husking seeds (De Nagy Koves Hrabar and Perrin 2002), seed size may be expected to affect seed handling and preferences differently than in most species studied previously.

The overall goal of this project was to determine the effect of seed size on food selection by Mourning Doves (*Zenaida macroura*) and Eurasian Collared-Doves (*Streptopelia decaocto*). Eurasian Collared-Doves are recent exotic invaders of North America, and may compete for food or other resources with native species, such as Mourning Doves, to the detriment of native species (Romagosa 2002). Bill-size-related differences in seed-size selection between Eurasian Collared-Doves and Mourning Doves may mitigate competition between these species for food resources, however (Poling and Hayslette 2006). Subdivision of food resources among sympatric avian granivores often is based on bill-size-relat-

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ed differences in seed-size selection (Grant 1986, Faaborg 1988, Ricklefs 2001). Mourning Dove bill length averages $12.83\text{--}14.53 \pm 0.97\text{--}1.01$ mm (Mirarchi and Baskett 1994), whereas collared-dove bill length averages 16.9 ± 0.71 mm for males and 16.6 ± 1.02 mm for females (Romagosa 2002). Corresponding differences in seed-size selection patterns between these species may have important implications regarding dietary overlap and competition, and ultimately, coexistence of the two species.

In cafeteria trials, previous work has indicated that Mourning Doves and other dove species prefer small, round seeds such as white proso millet (*Panicum miliaceum*; Hayslette and Mirarchi 2001, De Nagy Koves Hrabar and Perrin 2002), and consume relatively few large-seeded species such as corn (*Zea mays*) and sunflower (*Helianthus annuus*; LeBlanc and Otis 1998, Hayslette and Mirarchi 2001). These results appear enigmatic, as wild Mourning Doves are known to exploit corn and sunflower as important food sources (Lewis 1993). De Nagy Koves Hrabar and Perrin (2002) concluded that among Diamond Doves (*Geopelia cuneata*), seed size becomes a limiting factor above a threshold size, but below that threshold, size is of little importance in food handling and selection. I hypothesized that seed size has little influence on Mourning Dove selection of small seeds, but that preferences for, and consumption of, larger seeds, such as corn and sunflower, are limited by seed size. Based on this hypothesis, I predicted that Mourning Doves would preferentially select smaller than average corn seeds, and that this within-seed-type selectivity for size would decrease with progressively smaller seed types. I also hypothesized that Eurasian Collared-Doves are less limited than Mourning Doves by size of corn and sunflower seeds because their bills are larger; thus, they are able to exploit corn and sunflower food sources to a greater extent than Mourning Doves. Previous research has shown that Eurasian Collared-Doves consume more corn than Mourning Doves in cafeteria trials (Poling and Hayslette 2006). Based on this, I predicted that Eurasian Collared-Doves would show less within-seed-type selectivity for smaller corn and sunflower seeds than Mourn-

ing Doves, and would select larger corn and sunflower seeds than Mourning Doves.

METHODS

The first phase of this research was conducted at the captive Mourning Dove research facility at Auburn University, Alabama, from June to August 2000. I used 15 2nd-year Mourning Doves, captured as immatures on the university campus during the previous breeding season; doves were initially housed and cared for according to Mirarchi (1993). Prior to feeding trials, doves were fed an equal mixture (by volume) of the four foods used in feeding trials (described below) plus proso millet and browntop millet (*Panicum fasciculatum*). I randomly assigned doves to five flocks of three birds each, and each flock was used in a 20-hr feeding trial in a $3.7 \times 7.3 \times 2.0$ -m outdoor aviary. During each trial, doves were offered 200 seeds of each of four species—corn, black-oil sunflower, milo (*Sorghum vulgare*), and wheat (*Triticum aestivum*). Trials were preceded by ≥ 24 -hr acclimation periods, during which doves were fed an equal mixture (by volume) of test seeds only, followed by 24-hr fasting periods. Prior to each trial, I estimated size of seeds offered using a sample of 20 seeds drawn at random from each 200-seed batch. I attempted to insure that sizes of seeds in samples were representative of those in feeding batches by comparing the mass of each sample to the mass of the batch from which it was drawn. Because I sampled 10% of each batch (20 out of 200 seeds), mass of a representative sample would be 10% of the mass of the batch from which it was drawn. Thus, a sample was deemed representative and used if the ratio of sample mass to batch mass was 0.100 ± 0.003 . If not, the sample was returned to the batch and redrawn. Using digital calipers, I measured length, breadth, and thickness (corresponding to the longest, intermediate-most, and shortest dimensions, respectively; Greig-Smith and Crocker 1986) of each seed in each sample to the nearest 0.1 mm. Seeds of each species were then hand-scattered on a separate wooden seed tray ($41 \times 41 \times 4$ cm) filled with commercially available topsoil; trays were randomly arranged in a 2×2 arrangement on the floor of the aviary, with 1.8 m between adjoining trays. After allowing doves

to forage from the trays for 20 hr, I removed the trays and removed and counted the seeds that remained on the trays. If ≥ 20 seeds remained, I estimated size of seeds remaining in the batch using a sample of 20 seeds as before the trial. Analogous to pre-trial sampling, post-trial samples were deemed acceptable based on comparisons of sample mass and batch mass. A sample was used if the ratio of sample mass to batch mass was within 0.003 of the ratio of sample seed number (20) to batch seed number. If not, the sample was returned to the batch and redrawn. I compared number of seeds consumed among seed types using one-way analysis of variance (ANOVA) and Tukey's procedure. I calculated mean size of each pre- and post-trial sample with respect to all three size dimensions. I calculated the average size of seeds consumed with respect to each dimension for each seed type in each trial based on number of seeds consumed and pre- versus post-trial differences in average available seed size. The formula for this calculation is

$$S_e = \{(200 \times S_b) - [(200 - N_e) \times S_a]\} / N_e,$$

where S_e = average size of seeds eaten, S_b = average size of seeds prior to foraging (initial sample), S_a = average size of seeds not consumed, and N_e = number of seeds consumed. I then used a paired *t*-test—with trials as replicates—to compare mean size consumed with mean size available for each size dimension and each seed type.

The second phase of this research was conducted at the captive avian research facility at Tennessee Tech University during January–April 2004. I used 14 Mourning Doves and 13 Eurasian Collared-Doves captured during July–September 2003 in Coffee County, Tennessee. Methods generally followed those used previously, except as noted below. Individuals of each species were tested in a sequential manner in $2.4 \times 1.8 \times 1.8$ -m pens. Corn and sunflower seeds ($n = 200$) were presented to each individual in separate 5.5- and 4-hr trials, respectively; trials involving corn were longer due to the slower consumption of corn by both species. Trial order (i.e., seed type) was determined randomly for each dove, so that approximately half the individuals received corn first, and half received sunflower first. The two trials for each dove were inter-

ceded by 24-hr acclimation and fasting periods. Seeds were scattered in trays without topsoil. Pre- and post-trial seed sampling and measurements were conducted as in the previous trials, and similar analyses were conducted separately for each species, with individuals serving as replicates. Additionally, I used two-sample *t*-tests to compare the average length, breadth, and thickness of seeds, by seed type, that each dove species consumed. Trials in which doves consumed < 25 seeds were omitted from analyses because I suspected that dove foraging during these trials was too limited to allow for sufficient discrimination among available seeds. I did not conduct statistical comparisons of corn and sunflower consumption because trial length differed between seed types. I conducted all analyses using SAS/STAT (SAS Institute, Inc. 1990) and set $\alpha = 0.05$. All means are presented $\pm$ SE.

RESULTS

In the first phase (2000 Alabama study), consumption of seeds during trials varied among seed types ($F_{3,19} = 11.9$, $P < 0.001$). Doves consumed more milo, wheat, and sunflower (161.2 ± 24.3 , 142.2 ± 20.4 , and 103 ± 23.4 seeds, respectively), than corn (8.4 ± 3.0 seeds). Doves ate nearly all (198+) of the 200 milo seeds offered in three of five trials, and consumed almost no (≤ 2) corn seeds in two of five trials, so these seed types were excluded from further analyses. One trial, in which doves ate 198 wheat seeds, was omitted from analysis of wheat size consumption. Wheat and sunflower seeds consumed were average in size with respect to all dimensions (Table 1).

In the second phase (2004 Tennessee study), Mourning Doves consumed 24.9 ± 4.1 corn and 50.1 ± 10.3 sunflower seeds, and Eurasian Collared-Doves consumed an average of 47.0 ± 4.9 corn and 52.5 ± 8.7 sunflower seeds during trials. Two collared-doves and eight Mourning Doves ate < 25 corn seeds, and one collared-dove and four Mourning Doves ate < 25 sunflower seeds; these doves were not included in seed-size analyses. Both Mourning Doves and Eurasian Collared-Doves selected smaller-than-average corn seeds with respect to length and breadth (Table 1). Mourning Doves consumed corn seeds

TABLE 1. Measurements (mm) of seeds initially available to, and consumed by, Mourning Doves (MODO; 2000 and 2004) and Eurasian Collared-Doves (EUCD; 2004) in seed-size selection trials on captive birds in Tennessee and Alabama.

Year	Food	Dimension	Species	n^a	Initially available		Consumed		t^b
					Mean	SE	Mean	SE	
2000	Wheat	Length	MODO	4	6.3	0.1	6.4	0.2	-0.9
		Breadth	MODO	4	3.1	0.0	3.1	0.0	0.3
		Thickness	MODO	4	2.6	0.0	2.5	0.0	1.3
	Sunflower	Length	MODO	5	9.8	0.1	10.3	0.5	-1.1
		Breadth	MODO	5	5.2	0.1	5.0	0.2	2.6
		Thickness	MODO	5	3.1	0.1	2.7	0.3	2.0
2004	Corn	Length	MODO	6	12.7	0.1	12.3	0.1	4.3 ^c
			EUCD	11	12.7	0.1	12.1	0.3	2.7 ^c
		Breadth	MODO	6	8.4	0.1	7.9	0.2	6.1 ^c
			EUCD	11	8.4	0.0	7.6	0.2	5.3 ^c
		Thickness	MODO	6	4.5	0.1	4.6	0.3	-0.3
			EUCD	11	4.6	0.1	5.2	0.2	-3.0 ^c
	Sunflower	Length	MODO	10	10.4	0.1	10.5	0.3	-0.4
			EUCD	12	10.2	0.1	10.2	0.4	0.2
		Breadth	MODO	10	4.9	0.0	5.0	0.3	-0.1
			EUCD	12	4.9	0.1	5.8	0.3	-3.0 ^c
		Thickness	MODO	10	2.9	0.0	3.0	0.3	-0.3
			EUCD	12	2.8	0.0	3.5	0.2	-3.5 ^c

^a Sample size (n) equals number of three-bird flocks in 2000, individual doves in 2004.

^b t -values from paired t -tests comparing sizes of seeds initially available and seeds consumed; $df = n - 1$.

^c $P < 0.05$.

of average thickness, but collared-doves selected corn seeds that were thicker than average. Mean size of corn seeds consumed by the two species did not differ with respect to length, breadth, or thickness ($-1.0 \leq t_{15} \leq 2.8$, all $P \geq 0.11$). Mourning Doves consumed sunflower seeds that were of average size with respect to all dimensions, and average length, breadth, and thickness of sunflower seeds consumed were similar (within 0.3 mm) to average sizes consumed by Mourning Doves in the 2000 study. Eurasian Collared-Doves consumed sunflower seeds of average length, but selected seeds of larger than average breadth and thickness. Mean size of sunflower seeds consumed did not differ ($-0.7 \leq t_{20} \leq 1.6$, all $P \geq 0.12$) between dove species with respect to any dimension.

DISCUSSION

Results suggest that seed length and breadth limit Mourning Dove consumption of corn; seed thickness seems less important in selection. If seeds such as corn are oriented lengthwise as they are swallowed, it seems logical that the smaller of the two cross-sectional dimensions (thickness) would be less important

in determining ease with which seeds are swallowed. Thickness seems important, however, in species that husk seeds before swallowing. In a similar study of Eurasian Bullfinches (*Pyrrhula pyrrhula*), sunflower seeds consumed were 4.6% thinner, 3.1% narrower, and 2.1% shorter than average (Greig-Smith and Crocker 1986). Willson (1972) concluded that Purple Finches (*Carpodacus purpureus*) selected seeds based on thickness rather than length. The sunflower seeds we used seemed to be below the size threshold suggested by De Nagy Koves Hrabar and Perrin (2002), above which size becomes a factor affecting dove seed handling and selection. We used seeds of black oil sunflower, a relatively small-seeded sunflower variety commonly used in food plantings for Mourning Doves in the southeastern U.S. These seeds were smaller than sunflower seeds used in previous studies (Hespenheide 1966, Willson 1972, Greig-Smith and Crocker 1986, Diaz 1990). As predicted, consumption of smaller seeds, such as milo and wheat, seemed unaffected by seed size. Preference by Mourning Doves for milo in this study agrees with preference patterns documented elsewhere (Poling and Hayslette

2006), and suggests that seed preference in this species may be based, at least in part, on seed size and/or shape. Selection patterns favoring small seeds have been documented in several studies of seed-husking species (Hespenheide 1966; Willson 1971, 1972; Keating et al. 1992), but De Nagy Koves Hrabar and Perrin (2002) suggested that dove food preferences are influenced more by seed shape than size; round seeds are handled more rapidly than, and preferred to, elongate seeds. Because milo was both the smallest and roundest of the seeds we tested, it is impossible to tell which of these seed characteristics actually influenced seed selection.

As with Mourning Doves, consumption of corn by Eurasian Collared-Doves seems limited by seed length and breadth. In contrast to Mourning Doves, however, Eurasian Collared-Doves were influenced by corn seed thickness, choosing thicker-than-average seeds. If seed thickness is relatively unimportant in determining handling and/or swallowing efficiency, as postulated earlier for Mourning Doves, perhaps the Eurasian Collared-Dove's selection of thicker seeds increases foraging efficiency by increasing nutrient intake (benefit) per unit handling time (cost) (Stephens and Krebs 1986). Likewise, selection of broader- and thicker-than-average sunflower seeds may increase foraging profitability of Eurasian Collared-Doves. Selection for large foods, presumably to maximize foraging profitability, has been reported in other seed-eating birds (Myton and Ficken 1967, Ramos 1996).

Selection of larger than average corn and sunflower seeds with respect to certain dimensions by Eurasian Collared-Doves, but not by Mourning Doves (paired *t*-tests), suggests that collared-doves select thicker corn seeds, and broader and thicker sunflower seeds, than do Mourning Doves. Although direct between-species comparisons of average seed sizes consumed failed to reveal any such differences, the average corn seed consumed by collared-doves was 0.5 mm thicker than that eaten by Mourning Doves, and the average sunflower seed consumed by collared-doves was 0.8 mm broader and 0.5 mm thicker. Selection for larger seeds by Eurasian Collared-Doves than by Mourning Doves likely is related to differences in their bill sizes (Hespenheide 1966, Myton and Ficken 1967, Willson 1972).

Previous authors have expressed concern about how the recent Eurasian Collared-Dove invasion of North America may affect native species, particularly ecologically similar species, such as the Mourning Dove, with which Eurasian Collared-Doves may compete (Romagosa and McEneaney 1999, Romagosa and Labisky 2000, Romagosa 2002). A recent study of food-selection patterns of these two dove species revealed a high degree (95%) of dietary overlap between them (Poling and Hayslette 2006), although this was based on relative consumption of different seed types in a cafeteria experiment, rather than on size preferences within seed types. If genuine, the Eurasian Collared-Dove's preferences for seeds that are broader and/or thicker than those selected by Mourning Doves may result in differential exploitation of larger seeds, such as corn and sunflower, and concomitant mitigation of foraging competition between them. Partitioning of food resources among sympatric species based on seed size has been documented in a number of avian granivore communities (Grant 1986, Faaborg 1988, Ricklefs 2001). Similarly, limited foraging competition may mean greater potential for coexistence of Mourning Doves and Eurasian Collared-Doves than previously believed.

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